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## REDISCOVERY AND A REDESCRIPTION OF THE CROOKED-ACKLINS BOA, *CHILABOTHRUS SCHWARTZI* (BUDEN, 1975), COMB. NOV.

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**ABSTRACT.** The Crooked-Acklins Bank, a component of the southern Bahamas Archipelago, supports a terrestrial herpetofauna largely in common with other islands in the region, including a boid snake. This boa, *Chilabothrus chrysogaster schwartzi* (Buden, 1975), was considered a subspecies of the Southern Bahamas Boa complex (*Chilabothrus chrysogaster*), although the original description was based on limited specimen material. As the author of the original description used recently deceased specimens collected by locals, no description of living animals exists. Since its description in 1975 and the associated collection of four type specimens, no additional boas from Crooked-Acklins have been reported in the literature. In addition, to the best of our knowledge, no photographs of live specimens have been published, and no juveniles have been described. For these reasons, it has been suggested that the subspecies is either extremely rare or possibly extirpated from the bank. Here we report the first four living boas from the Crooked-Acklins Bank, including both juveniles and an adult. We present the first photographs of and morphological data from live wild specimens, including habitat descriptions and natural history observations. We conducted a phylogenetic analysis of these boas using maximum-likelihood and Bayesian approaches, as well as divergence time analyses, finding that the Crooked-Acklins Boa is a distinct species sister to the recently described Silver Boa (*C. argentum*), and is not closely related to *C. chrysogaster* populations. The distinctness of this taxon is also supported by known morphological and meristic characters. We describe the species as the Crooked-Acklins Boa, elevating the epithet *C. schwartzi* (Buden, 1975) **comb. nov.** to refer to boas of this genus from the Crooked and Acklins banks, Bahamas—the 13th species of *Chilabothrus*. We further assess the systematics

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of the Southern Bahamas Boa (*C. chrysogaster*) and the central Bahamas boas (*C. strigilatus*, *C. argentum*, and *C. schwartzi*) with novel sequence data for these lineages.

KEY WORDS: Boidae; Caribbean; *Chilabothrus*; mtDNA; phylogenetics; systematics

## INTRODUCTION

The West Indian or Greater Antillean boas (genus *Chilabothrus*) comprise a clade dating to a Miocene colonization of the proto-Antilles from South America (Reynolds et al., 2013). Twelve species are currently recognized, with eight species in the Greater Antilles (Cuba, Jamaica, Hispaniola, and greater Puerto Rico) and a further four species in the Bahamas (Lucayan) Archipelago (Sheplan and Schwartz, 1974; Schwartz and Henderson, 1991; Tolson and Henderson, 1993; Reynolds et al. 2016a). Despite a modest number of extant species, this genus has undergone remarkable morphological evolution, with deterministic processes repeatedly producing large generalist and small specialist species across several of the Greater Antillean island regions (Reynolds et al., 2016a). Further, this determinism in body size and ecological evolution has been arrived at via accelerated rates of head shape (trophic morphology) evolution as small-bodied species evolved from larger ancestors (Reynolds et al., 2016a).

In the Bahamas Archipelago, the four presently known extant species are largely restricted to their own island banks or series of island banks, and no two species co-occur. The Abaco Boa (*Chilabothrus exsul*), occurs in coppice habitat of Abaco Island and small satellites on the eastern Little Bahama Bank. The species is relatively small (max. snout-vent length [SVL] 888 mm) and terrestrial, although dietary habits are not well known. (Tolson and Henderson, 1993; Henderson and Powell, 2009). The Bahamas Boa (*C. strigilatus*) was recently split from the Hispaniolan Boa (*C. striatus*) owing to morphological and molecular phylogenetic

differentiation (Reynolds et al., 2013). This large-bodied, generalist species is restricted to the emergent islands of the Great Bahamas Bank and is found on large and developed islands such as New Providence, as well as on small cays such as the Exuma Cays. Five subspecies are presently recognized on the basis of morphological variation (mostly coloration; Sheplan and Schwartz, 1974), although molecular phylogenetic evidence might not support differentiation of these lineages (Reynolds et al., 2013). The Conception Bank Silver Boa (*C. argentum*) was recently discovered on the small (< 7 km<sup>2</sup>) Conception Island Bank (Reynolds et al., 2016b). A small-bodied arboreal specialist, the species is currently known from 43 individuals that have been observed (R.G.R., unpublished data) and is not thought to occur elsewhere in the region (Reynolds et al., 2016b). The Southern Bahamas Boa, as previously recognized, is a complex of three subspecies occurring on the Crooked-Acklins (*C. chrysogaster schwartzi*), Great Inagua (*C. chrysogaster relicquus*), Caicos (*C. chrysogaster chrysogaster*), and Turks banks (*C. chrysogaster chrysogaster*). This species is largely known from populations on the Caicos Bank, where the species has been well studied (Reynolds, 2011; Reynolds and Gerber, 2012). Only three individuals have been previously described from the Turks Bank (Reynolds et al., 2011), and the species is likely restricted to small offshore cays there. On the Caicos Bank, the species occurs on at least nine islands, occasionally at high densities (Reynolds and Gerber, 2012). The Inagua Boa (*C. chrysogaster relicquus*) is known from only five specimens and was previously thought to



Figure 1. Holotype specimen of the Crooked-Acklins Boa (*Chilabothrus schwartzi*). This specimen is accessioned in the Louisiana State University Museum of Zoology (LSUMZ 27500) as the holotype for *Chilabothrus chrysogaster schwartzi*.

have been extirpated from Inagua (Barbour and Shreve, 1935), although individuals have been recently observed (J.P.B., personal observation) and the apparent rarity is likely not a sign of near extirpation. The Crooked-Acklins Boa, *C. chrysogaster schwartzi* (Buden, 1975), was described from only four known specimens (Buden, 1975; Fig. 1; details below), none of which was seen alive by the researcher, and is thought to be restricted to Crooked and Acklins islands in the southern Bahamas. No specimens have been reported in the literature since Buden (1975), and no published photographs of these boas exist. It has been suggested informally by some Bahamian naturalists

that the Crooked-Acklins Boa might have been extirpated, although anecdotal reports of “large snakes” occasionally surface (R.G.R., personal observation). Nothing is presently known regarding juveniles, habitat selection and use, or natural history of these boas.

Here, we report on fieldwork conducted on Crooked Island, including the observation of four boas (three juveniles, one adult). Our analysis of morphological and genetic data demonstrates that the Crooked-Acklins Boa is a unique species, and we additionally provide detailed descriptions and photographs of this poorly known boa.

## METHODS

### Study area

The Crooked-Acklins Bank consists of a shallow carbonate platform approximately 2,600 km<sup>2</sup> in area (Sealey, 2006; Rankey, 2014). The bank is in the southern Bahamas Archipelago, surrounded by the Great Bahamas Bank (50 km west), Samana Bank (34 km north), and Plana Cays Bank (20 km east). There are two large islands on the bank: Crooked Island (252 km<sup>2</sup>, maximum elevation = 35 m above sea level [a.s.l.]) and Acklins Island (497 km<sup>2</sup>, maximum elevation = 36 m a.s.l.). Other larger islands supporting terrestrial herpetofauna in the Crooked-Acklins Bight are Long Island, North Cay, Fish Cay, the Guana Cays, and Castle Rock. These islands contain the majority of the habitat types represented in the Bahamas Archipelago (*sensu*: Correll and Correll, 1982) from mangrove to closed-canopy hardwood coppice, with the exception of mature mahogany (*Swietenia mahagoni*) and pineland (*Pinus caribaea*) forests, which do not occur in any abundance on the islands. As the Bahamas Archipelago is characterized by a reduction in rainfall from northeast to southwest (Knapp et al., 2011), the Crooked-Acklins Bank is more xeric (average rainfall < 900 mm per annum) than other islands on the Great (1,000–1,350 mm) and Little (1,500 mm) Bahamas banks (Inter-American Institute for Cooperation on Agriculture, 1989).

### Surveys

We conducted fieldwork over the course of 5 days on Crooked Island on 14–18 July 2017. We focused diurnal surveys on identifying potential habitat where boas might be likely to occur, and then focused nocturnal surveys in areas deemed to be best-quality habitat on the basis of our work on other

Bahamian boas (e.g., Reynolds and Gerber, 2012; Reynolds et al., 2016a,b). Nocturnal surveys of three selected sites consisted of walking slowly, searching for boas on the ground and in the trees using 1,000-lumen headlamps. Site 1 consisted of a closed-canopy forest at the base of a hill surrounding a freshwater well, a habitat type that is used by *C. chrysogaster* on both the Inagua and Caicos banks (R.G.R. and J.P.B., personal observations). Site 2 was a heavily disturbed coppice forest penetrated by a rough-cut dirt road near the highest point on Crooked Island (elevation ~32 m). Site 3 consisted of well-drained intact scrub forest on a small karst hill (elevation 22 m) ringed by closed-canopy coppice forest at the base of the hill. This site had many loose rocks and exhibited fewer signs of damage by Hurricane Joaquin. We intentionally refrain from providing more specific locality information owing to the sensitivity of these sites. During our first night, we conducted nocturnal surveys at the three sites, focusing subsequent efforts on Site 3 after discovery of the first boa.

In addition to surveys on Crooked Island, we also conducted a 24-hour survey on Fish Cay (22°29'23.9994"N, 74°15'W), a small (0.88 km<sup>2</sup>) low-lying (maximum elevation = 3 m a.s.l.) island located on the southern edge of the Crooked-Acklins Bank in the Bight of Acklins. This island, along with nearby cays, supports the only remaining populations of the endangered iguanid *Cyclura rileyi nuchalis* (Carter and Hayes, 1996; Buckner et al. in Powell and Henderson, 2012). Our hypothesis was that the continued existence of the iguanas on these cays might indicate that boa populations also occur there, as is the case for populations of *C. chrysogaster* on the Caicos Bank (Reynolds, 2011). Fish Cay is a sandy island, lacking exposed karst, with well-developed vegetation consisting of silver palms (*Coccothrinax argentata*), buccaneer

palms (*Pseudophoenix sargentii*), coccoloba (*Coccoloba uvifera*), mangroves (*Laguncularia racemosa*), and other associated vegetation. Portions of the northeast of the island are dense enough to be considered closed canopy, although the canopy is < 5 m high. Fewer than 12 small brackish ponds exist, as do the ruins of what was presumably a freshwater well. The island largely lacks typical refugia for terrestrial boas, other than abundant fallen palm fronds.

### Specimens

We hand captured boas, after photographing them in situ, and placed them into cloth bags for later processing. We measured mass to the nearest gram using a spring scale, and obtained SVL and tail length measurements to the nearest millimeter by extending a string along the dorsal surface of the extended snake. We obtained the following standard head measurements (e.g., Reynolds et al., 2016a): head width (widest head width); head length (anterior of the rostral scale to the posterior of the mandible); labial length (posterior-most supralabial scale to the anterior tip of the rostral scale); interocular length (narrowest distance between orbits); ocular length (horizontal diameter of ocular scale); nares–ocular length (anterior edge of ocular to posterior edge of nares); rostral–ocular length (anterior edge of ocular scale to anterior edge of rostral scale); internares length (narrowest internarial distance); and labial–ocular length (posterior edge of posterior supralabial scale to posterior edge of ocular scale). We used dial calipers for all measurements, rounding to the nearest 0.1 mm. We further obtained ventral and subcaudal scale counts, as well as head scalation from digital macrophotographs of all specimens. Finally, we obtained deoxyribonucleic acid (DNA) samples, consisting of 3–10 mm tail clips preserved in

95% ethanol. We sanitized tails before and after clipping and applied antiseptic dermal adhesive to prevent infection. We released boas at the exact point of capture, at night, less than 24 hours after initial capture. Thus, we obtained no whole-animal specimens, and instead have accessioned photographs into the Museum of Comparative Zoology (see below). We later extracted whole genomic DNA from tissue samples using the Promega Wizard SV DNA purification system and stored extracts at  $-20^{\circ}\text{C}$ .

### Previously known specimens

Before our fieldwork in July 2017, the Crooked-Acklins Boa was known from a total of four specimens (Table 1; Fig. 1) originally obtained (although not collected alive) by Donald Buden between 1972 and 1973 (Buden, 1975). The holotype for *C. chrysogaster schwartzi* (LSUMZ 27500) is the only intact specimen, and is a 785-mm SVL female from Delectable Bay, Acklins Island (Fig. 1). The second specimen (KUH 260082 paratype) consists of a portion of the dentary from an individual killed on Acklins Island. Specimen three (KUH 260083 paratype) is a mostly destroyed specimen, currently held together in cheesecloth, also collected on Acklins Island. The fourth specimen (KUH 260084 paratype), from Crooked Island, is just a head that was severed with a cutlass.

### Genetic data and analyses

To examine the phylogenetic relationships of the Crooked Island Boa, we used the polymerase chain reaction to amplify the mitochondrial (mt)DNA locus cytochrome B (*CYTB*), which has been shown to be useful in species identification in boas (Campbell, 1997; Burbrink, 2004; Reynolds et al., 2013). We conducted all reactions in SimpliAmp<sup>®</sup> (Applied Biosystems Foster City, CA) ther-

TABLE 1. KNOWN MUSEUM SPECIMENS REPRESENTING *CHILABOTHRUS SCHWARTZI*. ALTHOUGH SPECIMENS WERE ACQUIRED BY BUDEN (1975), ALL WERE COLLECTED FROM THE WILD AND KILLED BY LOCALS BEFORE BEING GIVEN TO D. BUDEN. ABBREVIATIONS ARE: ASFS = ALBERT SCHWARTZ FIELD SERIES; KUH = KANSAS UNIVERSITY HERPETOLOGICAL COLLECTION; LSUMZ = LOUISIANA STATE UNIVERSITY MUSEUM OF ZOOLOGY.

Institution	Specimen #	Field No.	Type	Locality	Condition	Collector
KUH	260082	ASFS V23916	Paratype	Delectable Bay, Acklins	Skull fragment only	Anon./Buden 1973
KUH	260083	ASFS V23917	Paratype	Delectable Bay, Acklins	Chopped up to pieces	Anon./Buden 1973
KUH	260084	ASFS V27420	Paratype	Cabbage Hill, Crooked	Head and neck only	Anon./Buden 1972
LSUMZ	27500	ASFS V27428	Holotype	Delectable Bay, Acklins	Entire, some machete cuts	Anon./Buden 1972

mal cyclers. We purified and sequenced products in both directions on an automated sequencer (ABI 3730XL) at the Genomic Sciences Laboratory at North Carolina State University, Raleigh. We assembled sequences and manually verified ambiguous base calls using Geneious 10.2.3 (Biomatters, Auckland, New Zealand). We then aligned sequences using the ClustaLW2 (Larkin et al., 2007) algorithm implemented in Geneious). We estimated a model of nucleotide substitution (HKY + I + G) using BIC in jModelTest2 (Guindon and Gascuel, 2003; Darriba et al., 2012).

We aligned these newly generated sequences with others representing all species of *Chilabothrus* (data from Reynolds et al., 2013, 2016a,b). To further contextualize the extent of genetic divergence among Bahamian species (Fig. 2), we also sequenced *CYTB* for the following species (see sampling locations in Fig. 3): *C. argentum* (11 novel sequences), *C. strigilatus* (19 novel sequences), *C. chrysogaster* (50 novel sequences), and *C. exsul* (12 novel sequences). We further added an additional 18 novel sequences from Hispaniolan *C. striatus*, as this species is closely related to Bahamian boas (Reynolds et al., 2013, 2016a).

We inferred haplotypes among our sequences of boas from the Bahamas Archipelago using FaBox 1.41. We calculated connection distances between these haplotypes using a pairwise distance minimum spanning network implemented in Arlequin 3.5.1.3 (Excoffier and Lischer, 2010). We removed sequences without precisely known provenance, including some sequences of *C. strigilatus* that were pet trade animals from Reynolds et al. (2013). We then reconstructed haplotype connections using HapStar (Teacher and Griffiths, 2010), and calculated pairwise corrected Tamura–Nei genetic distances between Bahamian *Chilabothrus* species using MEGA7 (Tamura et al., 2013).

We inferred a phylogeny of our boa haplotypes using a maximum-likelihood (ML) approach implemented in Geneious using the RaxML algorithm plug-in (Stamatakis, 2006). We used the GTRGAMMA model and the rapid bootstrapping algorithm with 1,000 bootstrap (BS) replicates followed by the thorough ML search option with 100 independent searches. We consider BS values above 70% to indicate relatively well-supported clades (Felsenstein, 2004).

To temporally contextualize divergence among lineages in the boa phylogeny, we estimated a time-calibrated mitochondrial



Figure 2. The other four species of boas found in the Bahamas Archipelago. A. adult female Conception Bank Silver Boa (*Chilabothrus argentum*) from Conception Island, Bahamas. Photo by J.P.B. B. young adult male Bahamas Boa (*C. strigilans*) from South Bimini, Bahamas. Photo by R.G.R. C. striped morph Turks Island Boa (*C. chrysogaster chrysogaster*) from Big Ambergris Cay, Turks and Caicos Islands. Photo by R.G.R. D. young adult male Abaco Boa (*C. exsul*) from Abaco, Bahamas. Photo by R.G.R.

coalescent tree for all species of West Indian *Chilabothrus*. As in previous studies (Reynolds et al., 2015, 2016b), we estimated a substitution rate for the mtDNA locus from the alignment of West Indian boas by constraining the root node of *Chilabothrus* using a normal prior with a mean of 21.7 Mya and a standard deviation of 1.8 Mya, derived from a fossil-calibrated divergence time analyses of the larger Neotropical boid phylogeny (Reynolds et al., 2013). We used the Bayesian Markov chain Monte Carlo (MCMC) method \*Beast (Heled and Drummond, 2010) implemented in Beast v1.8 (Drummond et al., 2012), running the MCMC for 100 million generations using a Yule speciation prior and an uncorrelated

lognormal relaxed clock model. We repeated the analyses three times with different starting parameter values, sampling every 1,000 generations and discarding the first 25% of generations as burn-in, to generate effective sample sizes larger than 200 for all parameters. We assessed convergence of the independent runs by a comparison of likelihood scores and model parameter estimates in TRACER v1.5 (Rambaut et al., 2013). We combined results from the three analyses using Logcombiner v1.8, and generated a maximum clade credibility tree using TreeAnnotator v1.8. We publicly accessioned the tree files in GitHub (<https://github.com/caribbeanboas>).

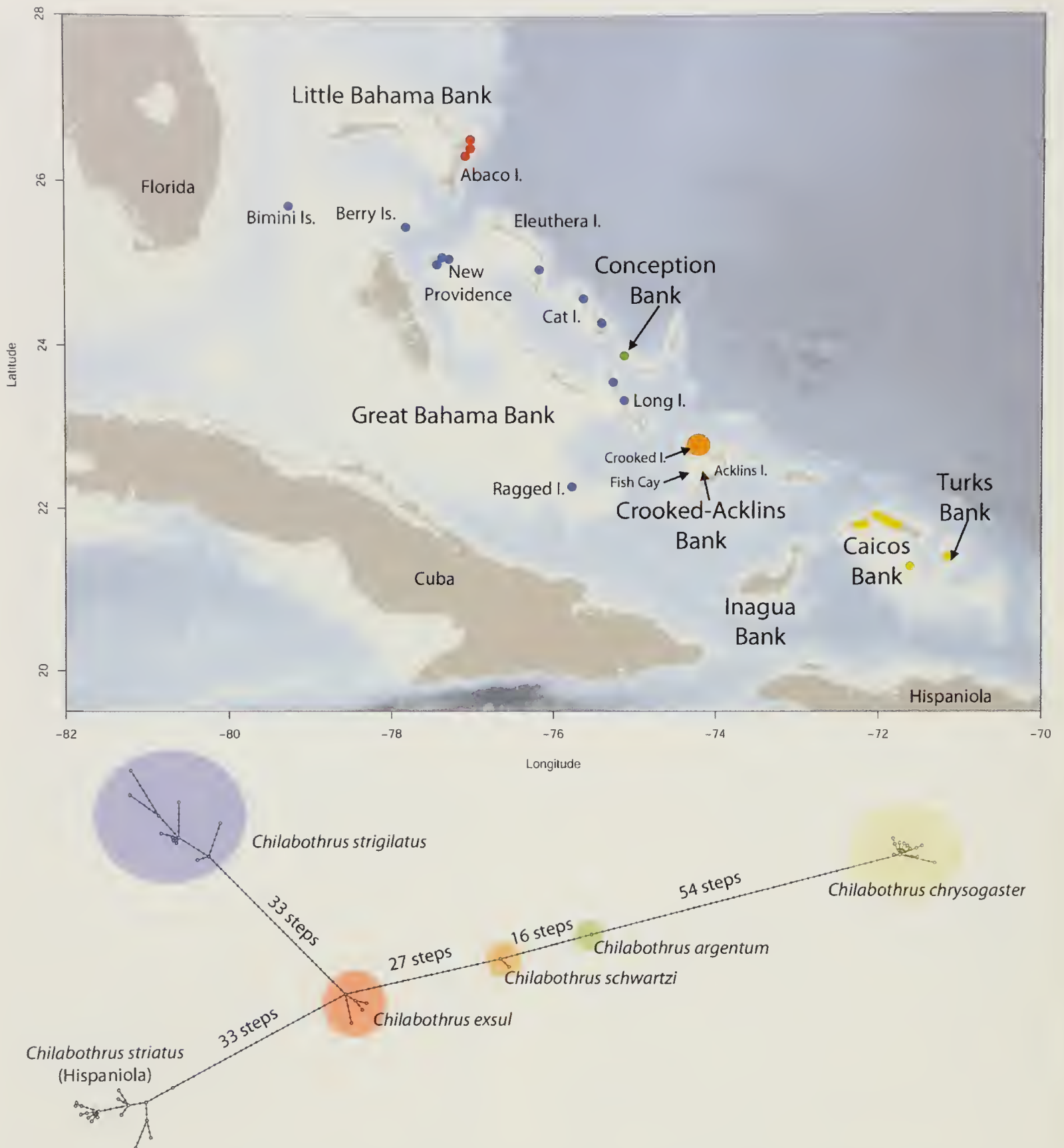


Figure 3. A, map of the northern Caribbean, including the Bahamas Archipelago. Island banks and island names discussed in the text are labeled. Bathymetric soundings are shown from light to dark blue. All sampling sites where boa samples were collected and used for genetic analysis are shown as circles, with colors corresponding to the five species of boas in the Bahamas and Turks and Caicos islands. B, median-joining network for the mitochondrial *CYTB* locus showing distances among species of boas in the northern Caribbean. Haplotypes from each species are enclosed in colored circles, with black dots representing mutational steps separating sequences. The minimum number of mutational steps among species is labeled.



TABLE 2. SPECIMEN DATA FOR FOUR INDIVIDUALS ENCOUNTERED JULY 2017. SPECIMEN NUMBERS REFER TO ACCESSIONED SPECIMEN VOUCHER PHOTOGRAPHS IN THE HARVARD MUSEUM OF COMPARATIVE ZOOLOGY. NO WHOLE-ANIMAL SPECIMENS WERE TAKEN. MCZ HO = MUSEUM OF COMPARATIVE ZOOLOGY HERPETOLOGY OBSERVATIONS; SVL = SNOUT-VENT LENGTH (MM); HL = HEAD LENGTH (MM); HW = HEAD WIDTH (MM); CO = CIRCUMORBITAL SCALES; SL = SUPRALABIAL SCALES; VT = VENTRAL SCALES; SC = SUBCAUDAL SCALES.

Specimen	Island	Sex	SVL	Tail	HL	HW	Mass	Loreal	CO	SL	VT	SC
MCZ HO 28	Crooked	F	523	120	18.6	8.4	30.5	2	9	13	—	—
MCZ HO 29	Crooked	M	525	116	17.9	8	32.5	1	8	13	—	—
MCZ HO 30	Crooked	M	576	130	19.6	9.6	40.5	1	8	13	—	—
MCZ HO 31	Crooked	F	774	168	24.5	12.1	95	1	9	13	—	—
KUH 260082	Acklins	—	—	—	—	—	—	—	—	—	—	—
KUH 260083	Acklins	—	—	—	—	—	—	—	—	—	—	—
KUH 260084	Crooked	—	“4–5 ft”	—	—	—	—	1	9	13	—	—
LSUMZ 27500	Acklins	F	785	175	29.1	17.7	—	1	10	13	277	95

## RESULTS

### Surveys

*Crooked Island.* Crooked Island was heavily damaged by a Saffir–Simpson category 4 hurricane (Hurricane Joaquin), which made landfall in late September 2015 and lingered in the area for 2 days. This caused extensive damage to the infrastructure of the island and created a significant amount of deadfall in the forests. This damage to the forest remained apparent on the western portion of the island, in particular, west of Colonel Hill airport, during our surveys in 2017. Thus, we limited searches to areas where the forest appeared to have been less damaged, as deadfall made moving through affected forests at night quite challenging.

We encountered the first boa (Museum of Comparative Zoology Herpetology Observations [MCZ HO] 28), a juvenile (Table 2), 1.5 m high in a tree on 15 July. The boa was actively climbing and presumably foraging. Boas two and three (MCZ HO 29–30, respectively), both juveniles, were also located while actively foraging about 1.5 m high in bushes the same evening. Boa two (MCZ HO 29) had an anole (likely *Anolis sagrei* on the basis of size, although we did not extract the item to confirm identity) in its stomach,

as determined by palpating the venter. We found the fourth boa (MCZ HO 31) on 16 July, an adult female crawling on the ground. These four animals (Fig. 4 A–D) were found within a 0.7 km by 0.4 km search area at Site 3. We did not observe boas at any other site, and we failed to find boas during a final search of Site 3 on 18 July. Our survey efforts of 56 person-hours thus yielded four boas, or 0.07 boas/hour.

*Fish Cay.* Our nocturnal surveys of Fish Cay on 17 July 2017 encompassed 16 person-hours, during which time we surveyed most of the island, including all major habitat types. We found no snakes, although the habitat and prey resources appear sufficient to support a population. Other squamate species are abundant there, including *Cyclura*, *Leiocephalus*, and *Sphaerodactylus*; although curiously we observed few *Anolis brunneus* relative to Crooked Island.

### Evolutionary relationships

We aligned a total of 1,077 base pairs of mtDNA from 58 haplotypes among 13 *Chilabothrus* taxa and four outgroups (*Eunectes* and *Epicrates*). All 17 sequences of *C. argentum* collapsed into a single haplotype, and we found at least two haplotypes for all other Bahamian taxa. Our ML and Bayesian

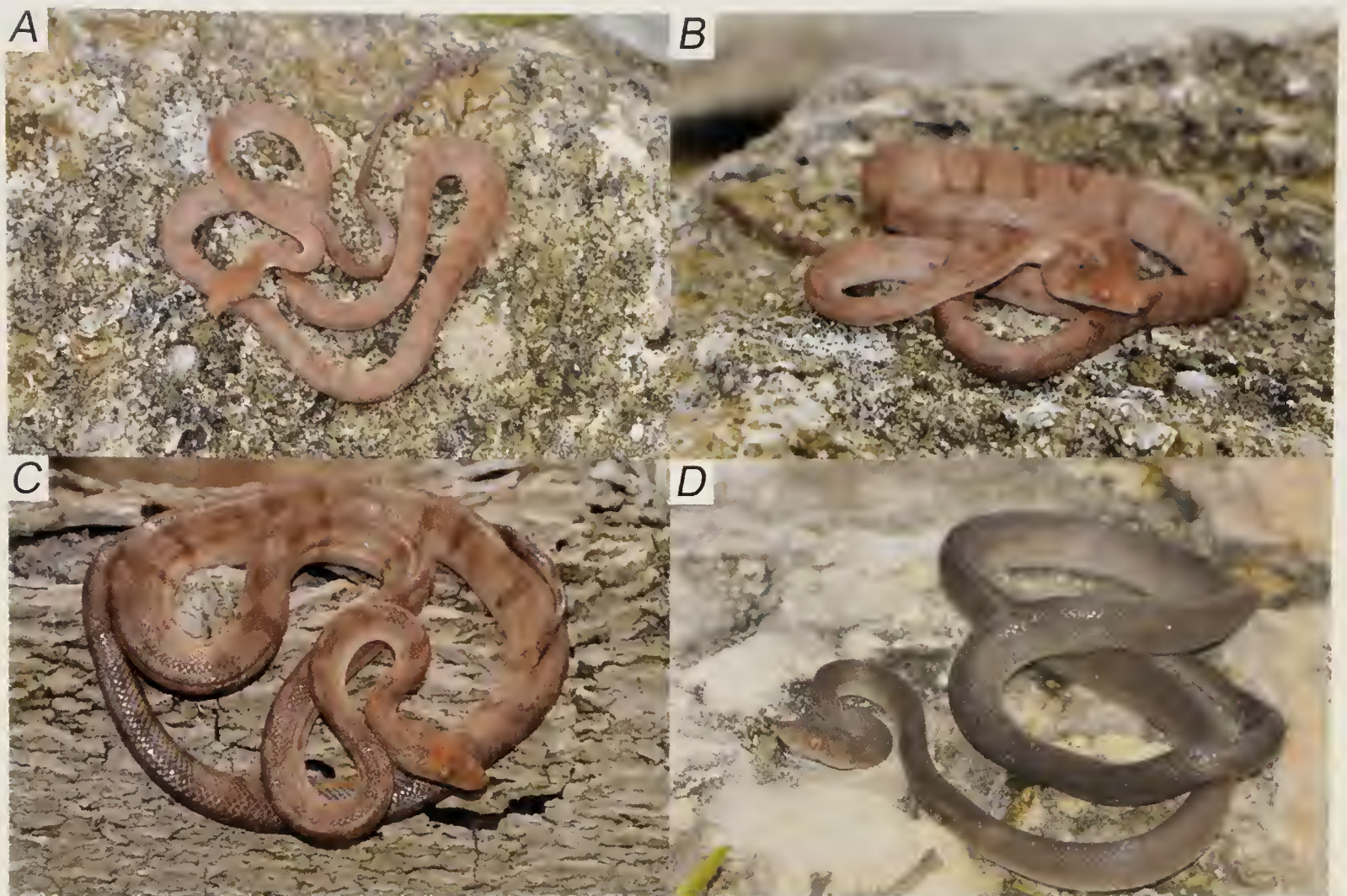


Figure 4. Four individuals of the Crooked-Acklins Boa (*Chilabothrus schwartzi*). A, a juvenile female, MCZ HO 28. B, a juvenile male, MCZ HO 29. C, a juvenile female, MCZ HO 30. D, a young adult female, MCZ HO 31. Photos by J.P.B.

phylogenies produced identical topologies with most nodes strongly supported (Fig. 5A), similar to previous studies (Reynolds et al., 2013, 2015, 2016a,b). We find that *C. chrysogaster schwartzi* is sister to the newly discovered *C. argentum* (Reynolds et al., 2016b) and is not closely related to *C. chrysogaster* (Fig. 5). We found moderate support for this topological arrangement (BS = 100; posterior probability = 0.89; Fig. 5) and a mean estimated coalescent time of 0.7 Mya (95% highest posterior density [HPD] = 0.0–1.4 Mya) for the two lineages. *Chilabothrus chrysogaster schwartzi* and *C. argentum* are together 1.7 Mya divergent from *C. exsul* (95% HPD = 0.5–2.9 Mya, Fig. 5), the next most closely related extant species. As in previous studies (Reynolds et al., 2013, 2015, 2016a,b), we find that the Bahamian

radiation of *Chilabothrus* was likely the result of at least two dispersal events from Hispaniola, as we find the Hispaniolan *C. striatus* nested within Bahamian species (Fig. 5A). Our haplotype network also supports the differentiation of *C. chrysogaster schwartzi*, which is 0.8% pairwise divergent from *C. argentum* (Fig. 3).

## DISCUSSION

Here we describe a new taxonomy for a previously recognized population of *Chilabothrus* boas in the Bahamas, designating the species *C. schwartzi* (Buden, 1975) **comb. nov.** Although the population was known on the basis of the descriptions of deceased individuals in Buden (1975), no subsequent specimens have been documented. We discuss

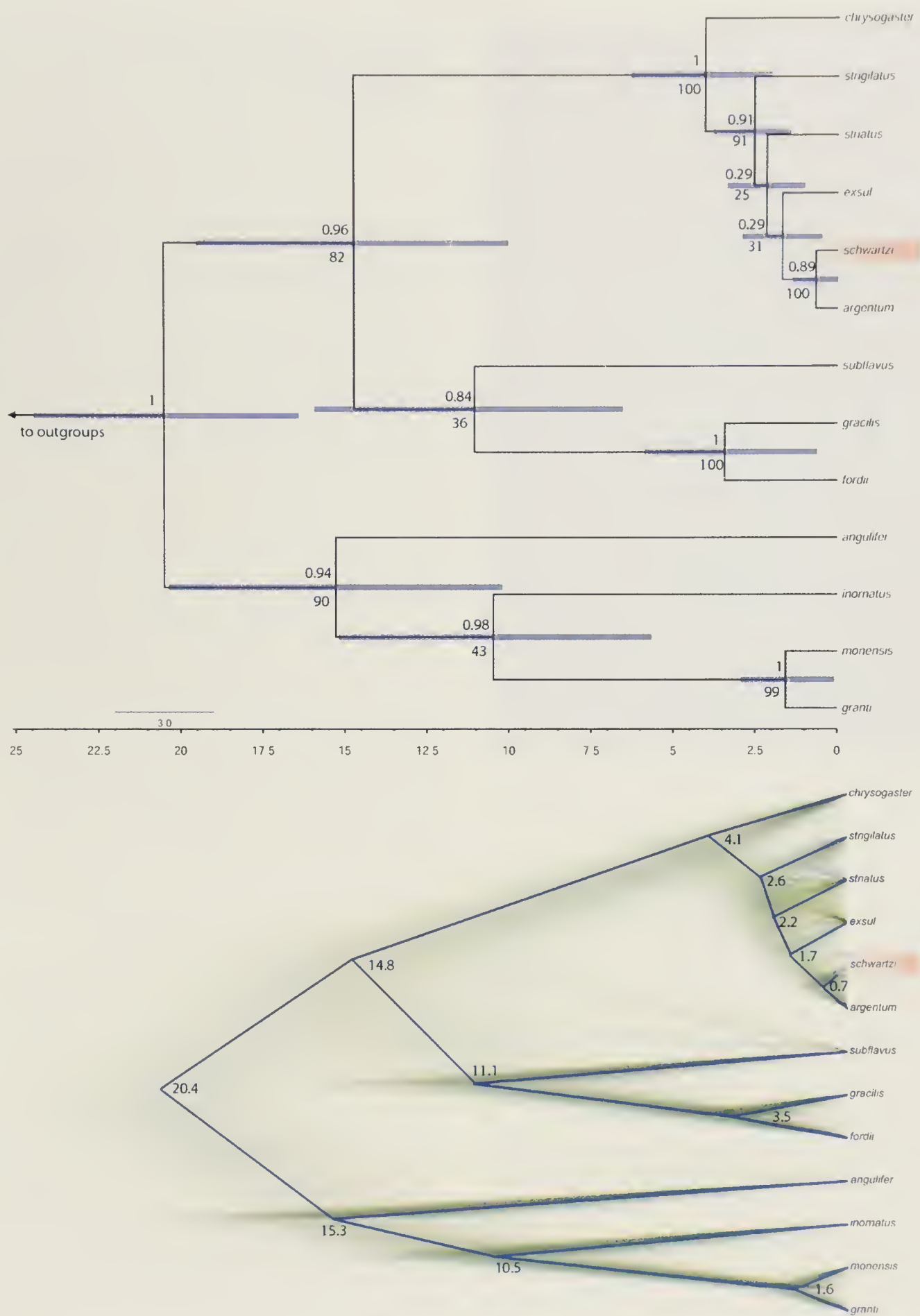


Figure 5. A, Bayesian ultrametric phylogenetic tree, inferred using \*BEAST, of the mitochondrial *CYTB* locus generated from all species of West Indian boas. Blue bars represent 95% highest posterior density intervals for coalescent time estimates, whereas numbers above the nodes represent Bayesian posterior probabilities and numbers below the nodes represent bootstrap values from 1,000 replications of a maximum-likelihood analysis using RaxML. The scale on the bottom shows coalescent time in Mya. B, density plot of all postburn-in trees from the Bayesian \*Beast analysis (~55,000 trees) showing variance in topological and coalescent time estimates. Nodes are labeled with mean coalescent times (in Mya) from the maximum-clade credibility tree generated from the time-calibrated analyses.

aspects of its natural history and evolutionary relationships below.

### Coloration

Unlike a previous report of this species suggesting that dorsal patterning coloration is a diagnostic character (Buden, 1975), we found an adult individual that largely lacked the dorsal saddle pattern, having just a faint suggestion of a pattern (Fig. 4D). This individual was nearly pure gray dorsally with a cream-colored venter and the top of the head had a rufous wash. The three juveniles we found all exhibited an orangish-red dorsal coloration typical of *Chilabothrus* species that undergo ontogenetic color change. As these individuals were only ~150 mm SVL shorter than the adult, we suspect that this ontogenetic color change might be delayed in this species, as snakes of this species tend to transition to the adult coloration about 1 year after birth (Reynolds and Gerber, 2012).

### Diet and behavior

We found all three juvenile boas actively foraging in arboreal situations. One individual contained a recent meal of an *Anolis* lizard, likely *A. sagrei*. These observations, combined with the small body size of the individuals, suggest that, like other *Chilabothrus* species, juvenile *C. schwartzi* are likely saurophagous and feed largely on *Anolis* lizards. There are two medium-sized arboreal *Anolis* lizards that occur on Crooked Island: *A. sagrei* and *A. brunneus*. Both were found to be abundant at Site 3 where we encountered the boas, and were easily located sleeping on leaves and terminal branches. Potential prey items for adult boas include *Leiocephalus* lizards (Reynolds, 2011; Buckner et al. in Powell and Henderson, 2012), birds, and introduced mice (*Mus* sp.). A single observation of a terrestrial-foraging

adult does not allow us to infer the typical foraging habitat of the species, although future work will seek to determine this.

### Evolutionary relationships and biogeographic implications

We find that *C. schwartzi* is sister to *C. argentum*, the latter of which occurs only on a single island ~130 km to the northwest. In a recent work describing *C. argentum*, it was suggested that the species likely occupied a larger area, possibly extending to the Rum Cay Bank to the southeast of the Conception Bank (Reynolds et al., 2016b). On the basis of the apparent shared ancestry of *C. argentum*, *C. schwartzi*, and *C. exsul*, we find that this group might represent an “eastern Bahamas” lineage that colonized the eastern edge of the Bahamas bank from Crooked-Acklins to the Little Bahama Bank. It is also possible that these boas existed on the Great Bahamas Bank, subsequently becoming extinct before or after the arrival of the ancestor of *C. strigilatus*. Further, these observations suggest that some in situ speciation in the Bahamian boas might have occurred, rather than repeated colonization of the region from Hispaniola.

### Southern Bahamas Boa (*Chilabothrus chrysogaster*)

*Chilabothrus schwartzi* was initially considered distinguishable at the subspecific level from *C. chrysogaster* on the basis of a higher number of ventral scales (based on one individual), one loreal scale, fewer supralabial scales, and more subcaudal scales (one individual; Buden, 1975). Further, they could be distinguished by the lack of a postorbital stripe and a distinct saddle pattern (Buden, 1975). These are not insignificant differences, which is why it is a bit surprising that Buden (1975) chose not to recognize the distinctiveness of the Crooked-

Acklins Boas from populations in Inagua and the Turks and Caicos, as the latter look very similar to each other. This was likely owing to the limited material available to Buden (1975).

Although *C. chrysogaster* was previously considered to be represented on the Crooked-Acklins Bank, we have demonstrated that that population is in fact a distinct species of boa sister to *C. argentum* from the Conception Island Bank. This leaves known representative populations of *C. chrysogaster* on the Inagua, Caicos, and Turks banks (Schwartz and Henderson, 1991; Reynolds, 2011, 2012). The former is recognized as the subspecies *C. chrysogaster relicquus*, whereas *C. chrysogaster chrysogaster* is known largely from the Caicos Bank, with a single known extant population on the Turks Bank (Reynolds and Niemiller, 2010; Reynolds et al., 2011). We do not yet have genetic samples from the Inagua population, but populations of *C. chrysogaster* on the Turks and Caicos banks are not deeply divergent from each other (Reynolds et al., 2011; Figs. 3, 5 this study).

#### Conservation concerns

This new species is apparently rare in the region, as few residents report seeing them and no wild specimens have been reported in the scientific literature in recent decades. Our surveys further suggest that the boas are confined to certain habitat types, in particular those with sufficient refugia and intact forest. Although the Crooked and Acklins islands are large in area, the amount of available habitat might be relatively small. Future surveys will focus on ascertaining whether this is the case. Additionally, introduced feral mammals, such as the abundant feral cats, are likely affecting the boa population, as in other regions (Reynolds, 2011).



Figure 6. A, close-up view of the head of a juvenile *Chilabothrus schwartzi*. Photo by J.P.B. B, in-situ photo of a juvenile *C. schwartzi* as discovered. Photo by A.R.P.-R.

#### Taxonomy

*Chilabothrus schwartzi* (Buden, 1975) **comb. nov.**

Crooked-Acklins Boa

Figures 1, 4, 6

ZooBank registration:

urn:lsid:zoobank.org:act:7C11C6DC-AF10-4BA0-819B-CA4E866C3991.

*Holotype*. LSUMZ 27500. An adult female collected in 1975 by D. Buden near Delcctable Bay, Acklins Island. Specimen measurements and meristics are listed in Table 2 and in Buden (1975).

*Paratypes*. KUH 260082–84. Three partial specimens of unknown sex, described in Table 2 and Buden (1975).

*Distribution.* Known from Crooked and Acklins islands on the Crooked-Acklins Bank, Bahamas.

*Definition.* A species of *Chilabothrus* boid snake with the following characteristics: no postorbital stripe, frequently (although not always) with elongated saddle blotches of slightly darker color than the dorsal ground color extending nearly to the ventral scales, immaculate cream-colored ventral scales, rufous dorsal head coloration, grayish-silver dorsal coloration in adults, reddish-orange dorsal coloration in juveniles, 1–2 loreal scales (modally 1 loreal), 8–10 circumorbital scales, 13 supralabial scales, possibly relatively higher number of ventral scales (277 in one individual; Buden, 1975), maximum SVL of at least 785 mm, and phylogenetic distinctiveness at the mitochondrial locus *CYTB* consisting of at least 0.8% pairwise divergence from other Bahamian *Chilabothrus* species.

*Ecology.* It appears that juveniles of this species are arboreal, and one individual juvenile was found to have consumed an *Anolis* lizard (possibly *A. sagrei*).

*Conservation.* This species is of unknown conservation concern, as too few individuals have been located and realized habitat use is unknown.

*Reproduction.* No reproductive information is available for this species.

#### CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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